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**Ecology of Plants  
in the Tropics**

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# 1 Vegetative Biology

## 1.1 Introduction

The vegetative parts of a tropical plant, just as with a temperate zone plant, are primarily adaptive in the context of gathering, storage, and manipulation of resources. These activities are carried out in an environment rich in Competitors, mutualists, herbivores, and variation in weather and soil. For example, most lowland tropical plants compete with individuals of other species and of many other life forms; most temperate zone plants have one or more conspecifics as nearest neighbours and the life forms of competitors are very monotonous. A number of tropical plants have mutualistic associations with ants, and the roots of many tropical plants have mutualistic mycorrhizal associations with fungi. Obligatory mutualistic associations with ants are absent from the temperate zones and while mycorrhizal associations occur, they are rarer. The tropical plant usually exists in a habitat that is far richer in species of herbivores and kinds of herbivory than that of the temperate zone plant. Within tropical habitats, the plant has to contend with mineral-poor soil and fluctuations in available water; important temperature change occurs within the 24-hour cycle and along elevational gradients. The mid-latitude counterpart often has mineral-rich soil and large fluctuations in temperature on a seasonal scale.

In tropical latitudes, there is a blurring of the distinction between the classical categories of plant vegetative-morphology-behaviour. For example, in the same habitat there are tree species that are totally deciduous during a six-month dry season, species that are completely evergreen, and species that drop their leaves in the rainy season and bear them during the dry season. In a 100 metre<sup>2</sup> area, life forms may range from vines to scandent shrubs, sprawling shrubs, upright shrubs, and small trees; some plants will start as shrubs and later turn into vines, and some vines become shrubs if deprived of support to climb. There are 'annual' plants whose 'year' is 40 years long (e.g., sisal, *Agave*), annual plants that grow a woody stem in less than a year, trees with a height increment of 4 metres a year and almost no woody tissue (e.g., papaya, *Carica*), and epiphytic herbs that live for tens of years without becoming woody. On the other hand, there are also habitats, such as mangrove swamps or high elevation oak forest where almost every plant is of the same life form.

Not only are there many behavioural and morphological life

forms within the tropics but, in addition, their proportional representation among the plant biomass and species changes from habitat to habitat. Vines disappear at high elevations, deciduous trees are rare on very poor soils, shrubs are rare in the understory of rain-forest, epiphytes are rare in certain deciduous forests, and so on. Sometimes these changes mimic those encountered in moving from the tropics to the mid-latitudes (e.g., vines are also a trivial portion of the species and biomass of northern forests) but the ecological causes may be unrelated.

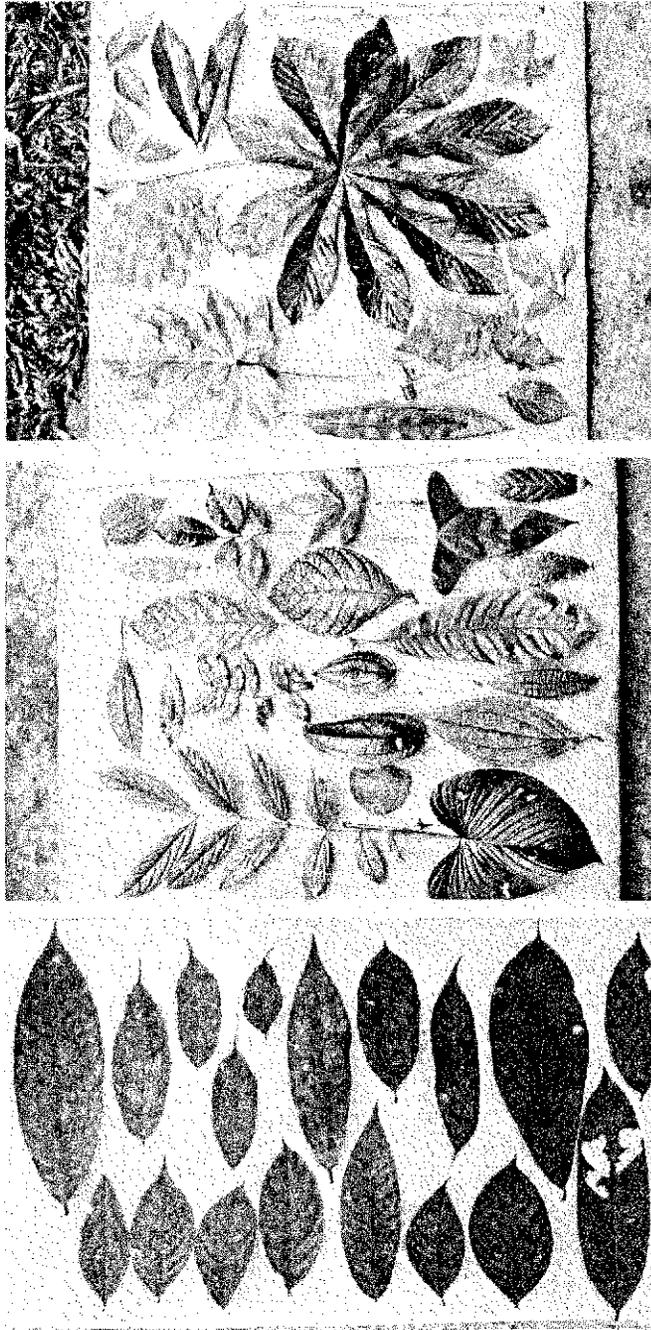
Only a few aspects of the vegetative morphology and behaviour of tropical trees have been chosen for discussion here. They were selected because a little is known about them or because they seem extraordinarily fertile areas for field research of the type that can be conducted on a miniscule budget.

### 1.2 Deciduous behaviour

Why do tropical trees discard their leaves at all? Why are they discarded at certain times and replaced at certain times? Generally, leaf drop is a response to (a) increased shading associated with competition within and between crowns, (b) damage caused by herbivores, wind or falling debris, or (c) dry weather.

In evergreen tropical habitats, the light falling on a leaf is reduced both when more leaves are added overhead in the same crown and when other crowns grow over the leaf. Leaf drop as a consequence of competition inside a crown is conspicuous in the tropics in fully insolated early successional vegetation. Here, where light is super-abundant and there is a premium on rapid vertical growth, leaves tend to be shed almost as soon as a shadow is cast on them. If minerals can be thoroughly extracted from leaves before discarding (or if the soil is rich in minerals), the cellulose skeleton that is lost means relatively little to the plant in a light-rich habitat. The lower leaves also provide attachment points for climbing vines, and so are in fact a strategic liability.

The monolayer crowns thus produced (e.g., *Cecropia*, *Macaranga*, *Ochroma*, *Piper*) are also encountered in the deep shade of evergreen forest understory. Here, monolayer crowns occur on saplings of over-story trees and on those species that attain reproductive maturity in the shade. In this nutrient- and light-poor habitat, the plant probably maintains only the most efficient leaves. However, it should also be very slow to drop one leaf and replace it, as the plant is either adapted to the low light intensity (an understory species) or 'waiting' for the sudden increase in light following a mature tree fall; in this heavily shaded circumstance, rapid vertical growth is less important



**Plate 1** (a) The leaves from the first 18 species of large shrubs and tree saplings encountered in a haphazard transect in an undisturbed rainforest understory. (b) and (c) The leaves from the first 31 species of large plants encountered in a haphazard transect in three-year-old secondary succession 100 metres from the collection site of the leaves in (a) (Finca La Selva, Puerto Viejo, Heredia Prov., Costa Rica, July 1973).



(a)



(b)



(c)

**Plate 2** (a) Tropical forest in the rainy season on foothills north of Tehuantepec, Oaxaca, Mexico. Juvenile columnar cacti grow well in the full insolation received when the trees are deciduous in the dry season; this is one of the few habitats where cacti can compete well with large leafy plants. (b) A representative rainforest tree with the rainforest recently removed (near San Miguel, Heredia Prov., Costa Rica); note irregular crown that once fit in with other crowns in the canopy. (c) Result of defoliation of a *Spondias* branch by Lepidoptera larvae early in the rainy season, leading to secondary production of leaves after the caterpillars have pupated (Alajuela, Costa Rica, late June 1973).

compared to the mineral and cellulose losses that occur when a leaf is replaced. In the understory habitat, it is therefore to be expected that natural selection influences the production of leaves that are especially resistant to herbivore and mechanical damage, and to the accumulation of epiphyllae. Without these three challenges, there is no obvious reason why an understory leaf should not live for many years (as indeed do the 3-7-year-old leaves of ericaceous evergreen shrubs in the understory of deciduous forests in the south-eastern United States). The phenomenon of epiphyllous plants (e.g., algae, lichens) accumulating on the horizontal leaves of rainforest understory plants is just a special case of inter-crown competition for light.

Inter-crown competition is of course a major aspect of the life of both juvenile and mature plants. When a juvenile is 'jockeying' for position in the canopy, leaf loss and replacement in almost all of the crown occurs in order to generate an optimal crown shape. Once established, however, it is probably only the crown margins which lose some leaves through shading. Again, this is a situation where, except for herbivore and mechanical damage, evergreen tropical leaves might be expected to live a very long time. Some overstory leaves last from less than a year to at least 3 years, but virtually nothing is known of the patterns of loss within the crown nor the causes for discarding leaves. It is known that there is great inter-specific variation in tolerance to shading by tropical tree leaves. One way this is expressed is by the commonly encountered inter-specific overlapping of tree crowns and the very graphic failure to overlap when two crowns of the same species happen to be side by side (they both have the same degree of shade intolerance). The multitude of shades of green encountered in tropical forest tree leaves is likewise probably associated with a wide range of shading tolerances.

Despite the observation that there is no conspicuous physiological reason for a mature tree in evergreen tropical forest to discard and replace most of its leaves, many do so. *Cordia alliodora*, a canopy-member tree, may be seen standing leafless for weeks in the middle of the rainy season in a Costa Rican rainforest that receives over 4 metres of rain evenly distributed through the year. High elevation Costa Rican oaks (*Quercus*) may be seen to drop their entire leaf crop and then within a few days to be covered with a crop of new bright red leaves. Bright 'Hushes' of pink, pale green, white or other oddly coloured new leaves can be seen dotting the upper surface of rainforest tree crowns at almost any time of year. It may be that the synchronization of entire crowns and entire populations, and the sudden protection of a small number of leaves in one cluster in one crown, are ways of escaping from herbivores. Otherwise, the herbivore population could easily build up on the new leaves if they were produced at a rate of a

few per day over a long time. It is also possible that leaf replacement in established crowns is necessary owing to accumulated herbivore and wind damage. Unfortunately, nothing is known of how much damage, and of which types a leaf can sustain before it is 'economic' to replace it with a new one. This may be a similar situation to that observed when comparing evergreen and deciduous species in tropical deciduous forest; the very durable leaf may last longer, but 'costs' more initially and is less efficient photosynthetically than the flimsy leaf. In evergreen tropical forests that are species rich, we should expect to find species at each of many points along the gradient between these two extremes.

In the progression from evergreen rainforest to habitats with long and thorough dry seasons (most of the lowland tropics are seasonal with respect to rainfall), the proportion of deciduous trees and species in the canopy overstory increases. In lowland habitats with more than four rainless months, almost all of the upland trees are leafless during most of the dry season (though both wind-free or upper elevation habitats require more dry weather for the same degree of leaf loss). However, if less than about 1.5 metres of rain falls in the wet season or if the soil fertility is very low, many lowland species remain evergreen throughout the year, leaf sizes decline, and stem-photosynthesizers (e.g., Cactaceae, Euphorbiaceae) become abundant.

Along watercourses in deciduous tropical forests, many of the woody plants retain their leaves during the dry season. Some of these belong to species that are deciduous on the dry hillside and evergreen when growing along the river, but other species are evergreen in either habitat. For example, in Costa Rica some of the evergreen tree species, such as *Hymenaea courbaril*, *Manilkara chicle*, *Curatella americana*, *Andira enermis*, *Trichilia* sp., and *Ficus* spp., synchronously dehisce their entire leaf crop during the middle or late dry season and then within a week or two produce another crop of equally drought-resistant leaves. Others, such as *Byrsonima crassifolia*, the palm *Acrocomia vinifera*, and the oak *Quercus oleoides* produce new leaves during much of the year.

The leaves of tropical plants that retain their leaves during most or all of the dry season are quite different from those of plants that have leaves only during the rainy season. Evergreen leaves are small (rarely more than about 6 centimetres long and 4 centimetres wide), leathery, simple, comparatively free of insect damage, and rich in secondary compounds. The latter trait is not surprising because in the tropical dry season, the herbivorous animals are active until they run out of food. Furthermore, the shade cast by evergreen trees on hill-sides and river bottoms is a major microhabitat in which many herbivorous invertebrates and vertebrates survive the dry season. The crowns

of evergreen trees are much denser and more globular than those of deciduous species (which have crowns like those found on elms, oaks and maples in mid-latitude forests), and they cast much heavier shade. During the rainy season, with its lower light intensity owing to cloudy weather, this may result in sub-optimal efficiency by the lower leaves in the crown. During the dry season, however, the very intense and unobstructed sunlight undoubtedly penetrates more deeply into the crown. In addition, a deep crown receives light laterally through the crowns of adjacent leafless trees. *Jacquinia pungens*, an understory small tree in Central American deciduous forest, has carried this behaviour to an extreme. During the rainy season it is leafless. During the dry season its dense and multi-branched crown bears thousands of small, leathery and very poisonous leaves. It has no surface roots but an extremely deep tap root. *J. pungens* lives in a seasonally available desert.

Even those trees in habitats with a predictable dry season may be damaged by dry weather. If the dry season is exceptionally dry, an evergreen tree such as *Hymenaea courbaril* produces undersized leaves, presumably because not enough moisture is available for their full expansion when young. As a consequence, it probably suffers sub-optimal photosynthesis during the following year. If the rainy season starts and then stops for 4 to 6 weeks, as it did in 1971 in Guanacaste Province, Costa Rica, deciduous tree species often lose their new leaf crop, suffer severe branch mortality, and then may not bear seeds for as long as 3 years (e.g., as did *Bombacopsis quinata*, *Ceiba pentandra*, *Enterolobium cyclocarpum*, *Pithecellobium saman*, *Tabebuia rosea*). This same drought caused all the *Hymenaea courbaril* to abort their fruit crops. This behaviour by *H. courbaril* underlines the concept that it is not the dry weather *per se*, but rather the energy loss from failure of photosynthesis, that is detrimental.

The observations above suggest intriguing complications when there are two similar and intense dry seasons each year (as in Colombia on the equator). Here, the deciduous species cannot be expected to produce two separate leaf crops (one for each rainy season) since the 'return' would probably not repay the original 'investment'. It is possible that the plants have to develop a more drought-resistant leaf so as to be evergreen during at least one of the dry seasons. Such a plant should have a lower net productivity than would a deciduous species in an area with one long dry season. Furthermore, certain strategies appear unavailable to such a plant. For example, it might have difficulty setting fruits in one dry season and then retaining them for a full year before maturing them, a feature that is common among trees at higher tropical latitudes (e.g., *Cassia grandis*, *Enterolobium cyclocarpum*, *Hymenaea courbaril*, *Swietenia macrophylla*).

Synchrony in discarding leaves may be a simple outcome of at least

three processes. First, many deciduous trees in the tropical forest may find that leaf retention is uneconomical at about the same degree of environmental dryness; this kind of synchrony should be strongly disrupted by local differences in drainage, wind exposure, soil fertility, and plant health. Second, as the various species become deciduous as the dry season approaches, any one tree need not retain its own leaves for 'ownership' of its crown space. Third, as the green foliage begins to disappear from the community, those species lacking exceptional herbivore defences will most probably receive exceptionally heavy damage to their remaining leaves. This third process leads to the intriguing question of why plants actively discard old leaves instead of simply allowing them to be eaten off. The answer must be that when a leaf is discarded, the plant has the chance to extract all possible nutrients from it. Synchrony of leaf production at the crown, population and community levels involves the inverse of these three processes.

### 1.3 Vines

Plants that use other plants for support and have elongate stems that invade other crowns, hereafter called 'vines' (= herbaceous and woody lianes), are the most poorly understood of all the major tropical angiosperm life forms. Though a woody vine may bear a crown as extensive as that of a large tree, vines have no commercially important wood (except for rattan palms) and thus have been of little interest to foresters. The reproductive biology of vines as a group is not unusual and thus they have escaped the attention of more esoteric biologists. For unexplained reasons, they constitute a trivial portion of temperate zone vegetation both in species and biomass. However, lowland tropical vegetation often abounds in vines. As vines rely on a rapid rate of elongation for their competitive advantage, they grow well in tropical habitats except where it is very dry or cool, or where the soil is very poor. Almost every habitat is distinguishable by the traits of its array of vines. Here, two rather different habitats will be discussed, but all tropical habitats need analysis of their vines for these and other traits.

#### 1.3.1 Early secondary succession in deciduous forest

In old fields, riversides, roadsides, swamp edges, landslide edges, etc., vines are prominent in the dry tropics. They grow rapidly during the rainy season and, with the exception of a few evergreen Bignoniaceae, are mostly deciduous. They are perennial and capable of rapid regeneration from cutting- and fire-resistant root stocks, and many of the species persist throughout many successional stages and

develop long woody stems. Most belong to the Apocynaceae, Aristolochiaceae, Asclepiadaceae, Bignoniaceae, Convolvulaceae, Dioscoreaceae, Euphorbiaceae, Fabaceae, Sapindaceae, and Vitaceae, families that are not well represented in temperate zone floras. When these families do occur at mid-latitudes, such as Fabaceae, Asclepiadaceae and Apocynaceae, most of the representatives are not vines. Tropical vines have crowns that rapidly and frequently shift location as they grow. The branches climb by twining, recurved hooks and many forms of tendrils (which commonly are modified leaves or leaflets). The leaves are often widely spaced along the branch and may form a close-fitting monolayer 'crown' over the substrate. When there is a shortage of substrate, they often climb on each other and disrupt the neat leaf arrangements encountered when inter-crown competition is less intense. Among the Fabaceae, there are even species that climb while deciduous; they move themselves well over the substrate plant's crown before producing leaves. They have only tiny leaves on the rapidly elongating branch and develop a leafy crown when the rains come.

Nutrient storage for sexual reproduction and production of new leaves is commonly accomplished with swellings of the roots and, in some cases, really large tubers. Sweet potatoes (*Ipomoea*) and yams (*Dioscorea*) are familiar examples. Presumably, the above-ground portion of the stem does not have an adequate volume for storage needs. In addition to being below the ground, tubers are generally well protected with chemical defences (see Chapter 4). They are found above ground only in habitats that lack a large biomass of animals (e.g., forests on white sand soil, forests at high elevations, and island vegetation).

Most species of vines in deciduous forest seem to adopt one of two different methods of crown production. Some have a few elongating branches that move far from the root stock before bifurcating to form a distinct crown (if they ever do). These species commonly have only a few chemically very well protected shoot tips, lose few shoot tips to herbivorous insects, and elongate relatively slowly. More commonly, vines produce many rapidly elongating branches close to the root crown. Many of these branch ends are eaten by herbivores before they grow more than a few metres. The former life form produces very diffuse crowns and is most abundant in areas that are infrequently disturbed; the latter life form produces very dense crowns and some such species may survive even if the area is cut or burned more than once per year.

Even the minute details of climbing can be of biological significance. A population of vines generally contains both right- and left-handed individuals with respect to the way they twine around the substrate;

in the northern hemisphere left-handed individuals have significantly larger seed crops than right-handed ones, and the effect is reversed in the southern hemisphere. Other 'handed' plants, such as coconuts, display the same phenomenon. It has been suggested that this is because the left-handed individuals have slightly more leaves exposed to the slanting sun's rays in the northern hemisphere than in the southern hemisphere.

The mechanically self-supporting plants of early secondary succession have a number of traits that minimize the chances of their being used as vine trellises. This protection can be most clearly demonstrated when a plant's vine defences are experimentally removed. For example, this occurs when the obligate acacia-ants are removed from a swollen-thorn acacia. These ants live in the thorns and kill any vine that starts to climb on the acacia. The acacia has many lateral branches at all heights, thorns and leaves angling upward from the branches, and compound leaves. The acacias without their ants rapidly become covered with vines while other species of self-supporting woody plants a few metres away are usually quite free of them. These other plants have smooth stems, downward pointing petioles bearing simple lanceolate leaves, and very few lateral branches within a metre of the central shoot tip. When a vine tendril or shoot tip contacts such stems, it often slides off. This leads to a mass of vines at the stem base. The shrubby acacia has a life form normally associated with more xeric habitats (that are relatively vine-free). It is of interest that where rivers run through relatively dry deciduous tropical forest, dry forest species with a shrubby life form occur near the river. While such a shrub grows very well, it often becomes a superb vine trellis and does not reach reproductive maturity owing to the inability of its crown to repel vines. Such an array of plants is an obvious candidate for some elegant experimentation.

### 1.3.2 *Undisturbed evergreen rainforest*

In the understory of evergreen rainforest on lateritic or on even better soils, woody vine stems up to 20 centimetres in diameter are a prominent part of the scenery. Free of leaves and low branches, they are the pipelines to crowns that may be nearly as large as the tree crowns that support them. A cross section of these stems shows them to consist almost entirely of water-conducting elements of very large diameter. Owing to the lack of wood deposition, they are impossible to age but it is clear from their population structure and physical locations that they are of ages equalling those of the trees that support them. Since they sprout readily from lateral roots (see section 1.4), the lineage represented by a plant may be even much older than its support. A crown of one

of these vines appears to be quite dynamic in location and may be as much as 100 metres from its roots. If one follows the stem out from the first point of connection with the ground, it may amble for a hundred metres or more across and through the litter, and be connected to other large stems reaching the canopy at 40 to 50 metres height. (Incidentally, this suggests that a vine has no chance of its roots recovering nutrients that are lost when it discards its leaves.) The arboreal stems may also loop from the canopy to the ground and back up, indicating that a tree fell out from under the stem long ago. By examining tree falls of various ages, all stages of a vine's growth strategy can be encountered, since new vertical shoots most commonly become established at such sites. When trees are felled, vines may even prevent the fall of a tree that has been cut at the base, owing to cross connections with other trees. Vine crowns blend in with the tree crowns to produce a more complete canopy than do the trees alone, and appear to have leaf exchange, branch development and sexual behaviour like that of the trees. In contrast with the vines of deciduous forest, many rainforest vines do not appear to have large storage tubers as mature plants. However, like forest trees, their root systems are essentially unknown.

Recruitment by the vine population is quite complex. In addition to the vegetative 'reproduction' to be discussed in section 1.4, they produce both large and small seeds, as do the trees. Behaviourally, the seedlings are quite different from tree seedlings. Some produce small understory shrubs that appear to be quite inactive for undetermined but long periods. During this time, a large tuber is growing on the tap root. Quite suddenly, the central axis begins to elongate rapidly, at a rate of as much as 5 centimetres per day. This rapidly climbing stem has very few leaves and if substrates are available, may climb at least 5 metres and probably much more without proliferating into the beginnings of a crown. During the period of intensive growth, the tuber becomes very soft and presumably exhausted of stored nutrients. In a habitat that contains very little sunlight for photosynthesizing, such a growth strategy is a way of attaining a high level in the forest while minimizing the amount of time that the succulent shoot tip is available to herbivores. A quite different set of species of vines simply start out as rapidly growing vine seedlings. They usually grow from seeds weighing as much as 20 grammes, and are nearly leafless for many metres. They put all their energy into vertical growth. For example, if growing in a dark room near a well lit window, a *Dioclea macrocarpa* seedling will grow past the window until it hits the ceiling, and only then turn back and try to grow out the window. Almost every 'young' vine of any size will be found to be connected by a lateral root to an established vine or root.

### 1.4 Vegetative reproduction

The growth patterns of tropical perennial plants suggest an intriguing problem and severely inadequate terminology with respect to the concept of 'vegetative reproduction'. Apomixis and other forms of asexual production of dispersable propagules do occur in the tropics, but the most conspicuous form of asexual multiplication is the production of long horizontal roots just below the soil surface, which in turn produce vertical shoots from some nodes. Sloppily called 'vegetative reproduction', we only apply this term because we cannot see underground. Such a plant is hardly doing more than producing a diffuse crown. At first, the new shoots are drawing on the established plant crown just as are the new branches that are produced in an arboreal crown when the rainy season starts. Even when the connection to the shoot is severed by herbivores or by the 'parent', this should not be regarded as an act of reproduction. The new shoot is no more the unit of selection than is a leaf in a tree crown. Evolutionarily, this type of growth should be viewed as a class of resource allocation whereby an established plant becomes huge and is not restricted to the location of the original seedling. Forest vines provide some of the best examples of this behaviour. If a habitat is populated by a large number of individuals produced asexually from one parent, and an event occurs that leads to differential mortality among them, it is directly analogous to predation on part of the worker ants in a colony, or to differential branch death owing to herbivory in a tree crown. Hard as it is to visualize, we may be dealing with the situation where the true reproductive population of a plant may be an extraordinarily small number of individuals, each of which is very large, perhaps numerous subdivided, and spread over many hectares.

The interesting question then is 'why is this form of crown expansion so abundant in the tropics?' A few answers may be formulated, but our knowledge of the biology of tropical wild plants is so primitive that they must at best be viewed as halting first steps.

First, year-round warm weather permits this behaviour. The new sucker shoot has the resources of the established plant to draw on rather than being confined to the small reserves that can be placed in a seed. It may continue to grow (and compete) well into the dry season and therefore this type of crown expansion can be used at almost any time of the year. In contrast, seedlings are much more restricted in the times at which they have any chance of survival. For example, if a patch of deciduous forest is cut during the late rainy season, many of the old root stocks immediately put up vigorous sucker shoots that grow and remain leafy throughout the dry season, while nearby adults of the same species are leafless and seedlings are dying of desiccation. Even without

cutting, the arboreal sucker shoots from horizontal subterranean roots may retain their leaves in the dry season while the established plant loses its leaves.

Second, a species-rich area of vegetation usually contains many diverse life forms and therefore may exhibit different kinds of competitive weakness. A plant may well be able to expand its crown more readily at various (and unpredictable) distances from the established crown than on the edge of the crown itself, as for example, when it is adjacent to particularly dangerous competitors or is being overtopped by a vine. In an environment containing highly heterogeneous resources, subdivision may be appropriate for a sedentary organism.

Third, in habitats where seedling establishment is extremely difficult, we may expect strong selection for great adult longevity and great adult size; generally, a plant with double the volume of canopy produces much more than a double-size seed crop. A plant may have to be huge before it can produce enough seeds to have the chance to make even one new reproductive adult. Once a tree is established, it may well be highly adapted to put part of its resources into sucker shoots rather than seeds, in order to increase both seed crop size and plant longevity. This selective pressure would, of course, become progressively weaker the greater the nutritional drain on the established plant of getting a sucker shoot to reproductive size. It is therefore not surprising to find that rainforest trees do not readily produce sucker shoots from stumps or roots, while rainforest vines and almost all woody plants of deciduous forest display this behaviour.

Some methodological comments can now be made. First, in habitats that man frequently burns, cuts, or grazes (but where roots are left intact), plants that root and stump sprout are more likely to survive. Since most of the easily accessible tropics are of this type, one can be quickly left with the illusion that all tropical plants do this all the time. This is clearly not the case in more natural circumstances, but we know so little about natural vegetation that it is hard to know how badly our view is distorted. The natural circumstances are of greatest importance in that they give us some idea of the selective pressures that led to the evolution of 'vegetative reproduction'. Second, to understand the phenomenon, we need some straightforward physiological descriptions of what stimulates a plant to produce sucker shoots at a particular time, and what prevents further resources from being put into a sucker shoot that is losing in competition or dying from herbivory.

### 1.5 Epiphytes

While conspicuously absent from the branches of mid-latitude forest

trees (with the exception of the bromeliad Spanish 'moss' (*Tillandsia usrinoides*) in the southern United States), small angiosperm herbs and shrubs growing epiphytically on tree crowns and trunks are a prominent portion of the biomass and even the species list of some tropical habitats. They are accompanied by ferns and a wide variety of primitive plants; only the latter groups do well in the temperate zones as epiphytes. In all but the very driest tropical habitats there are a few angiosperm epiphytes, but their biomass is greatest at upper intermediate to high elevations, where clouds press against the mountains most of the day, and they are most species-rich in low intermediate elevation rainforest with a mild dry season. The primary families are Gesneriaceae, Melastomataceae, Cactaceae, Rubiaceae, Asclepiadaceae, Solanaceae, Bromeliaceae, and Orchidaceae. The latter two families are almost entirely epiphytic and contain most of the angiosperm epiphytes in the Neotropics. Terrestrial (non-epiphytic) Bromeliaceae live mostly in xeric and very high elevation sites, and terrestrial orchids are high elevation and mid-latitude in distribution. Somewhat enigmatically, Bromeliaceae are absent from the Old World tropics; while various Old World ferns appear to be morphological analogues to bromeliads, there appears to be a very large amount of empty branch habitat. One hesitates, however, to suggest the obvious experiment of introducing bromeliads to the Old World because of the strong possibility of economic repercussion.

Clearly, The angiosperm epiphytic life form has evolved many times. Ecologically, an epiphyte is a perennial plant which does not have to produce and maintain massive woody stems and branches. However, it has to contend with an extremely nutrient-poor substrate (the roots are dependent on rain water, a small amount of litter fall, and material brought by animals) and a very erratic water supply (soaked when it rains, the plant lives in a desert when the wind blows). While the epiphyte's habitat is on average better insolated than is the forest floor, an individual epiphyte has little chance to shift its crown to avoid shading. On the other hand, once established on a branch, the chances are reduced of another plant growing up next to the adult epiphyte, if for no other reason than substrate is missing from most of its periphery.

The competitive interactions of epiphytes are complex, but probably amenable to analysis. C. Schnell, working with Central American epiphytes, finds that in habitats with up to 10 to 20 epiphyte species in at least three families, relatively distinct portions of the habitat can be identified for each species by recording the following kinds of simple parameters for each individual epiphyte: distance from the tree centre, height above ground, depth in the tree crown, distance to nearest con-specific, degree of shading of the branch, and angle of the supporting

branch. Most species of epiphytes produce very large numbers of very small and wind-dispersed seeds. Their successful germination and growth on a tree branch appears to be strongly influenced by competitors and the physical environment (as well as by mycorrhizal associations in some cases). In contrast to many other tropical associations of plants, it appears that epiphyte community structure may be little influenced by herbivory.

Epiphyte leaves are conspicuously much more evergreen than those of the plants on which they grow, apparently very desiccation resistant, and quite free from herbivore damage. In view of the nutrient-poor environment of epiphytes, it is likely that heavy investment in chemical defences of their few leaves is worthwhile (see Chapter 4). Like vines, most epiphytes are impossible to age because they do not lay down woody tissue. However, their very slow growth rate suggests that they live for tens of years. There are some individual bromeliads and orchids in Costa Rica that do not appear to have changed in size in the past ten years. They flower every year and as new leaves and short stems are added, the old ones rot off. Unless the branch falls off, there is no obvious reason why an angiosperm epiphyte should die once established, except through competition for light and exceptionally severe fluctuations in the physical environment.

### 3.6 Roots

In a system where most of the inorganic nutrients are in the living vegetation, it is not surprising to find that the roots compete strongly with the fungi, bacteria and litter animals for newly fallen litter. Inorganic material that finds its way to the soil is likely to be rapidly lost by leaching during the heavy rains of the rainy season. It is also not surprising to find that in such a system the roots are often involved in a mutualistic interaction with fungi that appear to be specialists at gathering minerals. Current studies in Costa Rican rainforest by D. Janos suggest that many rainforest tree roots may have virtually no root hairs, and depend entirely on mycorrhizal fungi for mineral uptake. The tree apparently provides carbohydrates to the fungus, which are taken up by the hyphae penetrating the roots, and the fungus moves minerals into the roots from its hyphae in the soil and litter. It may be significant that such associations seem to be best developed on tropical white sand soils (which have almost no physiologically useful minerals) and among epiphytic orchids, and to be most poorly developed in plants of early primary succession (e.g., *Cecropia*, *Ochroma*, *Trema*, *Urera*) that normally grow on soils enriched from fire ash, flood water soil deposition, or litter from a fallen tree.